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Land use changes could modify future negative effects of climate change on old-growth forest indicator species

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Abstract

Aim: Climate change is expected to have major impacts on terrestrial biodiversity at all ecosystem levels, including reductions in species-level distribution and abundance. We aim to test the extent to which land use management, such as setting-aside forest from production, could reduce climate-induced biodiversity impacts for specialist species over large geographical gradients.

Location: Sweden.

Methods: We applied ensembles of species distribution models based on citizen science data for six species of red-listed old-forest indicator fungi confined to spruce dead wood. We tested the effect on species habitat suitabilities of alternative climate change scenarios and varying amounts of forest set-aside from production over the coming century.

Results: With 3.6% of forest area set-aside from production and assuming no climate change, overall habitat suitabilities for all six species were projected to increase in response to maturing spruce in set-aside forest. However, overall habitat suitabilities for all six species were projected to decline under climate change scenario RCP4.5 (intermediate–low emissions), with even greater declines projected under RCP 8.5 (high emissions). Increasing the amount of forest set-aside to 16% resulted in significant increases in overall habitat suitability, with one species showing an increase. A further increase to 32% forest set-aside resulted in considerably more positive trends, with three of six species increasing.

Main conclusions: There is interspecific variation in the importance of future macroclimate and resource availability on species occurrence. However, large-scale conservation measures, such as increasing resource availability through setting aside forest from production, could reduce future negative effects from climate change, and early investment in conservation is likely to reduce the future negative impacts of climate change on specialist species.

KEYWORDS

Citizen science data, dead wood-decaying fungi, forecasting, forestry, habitat management, set-aside forest, species distribution models

1 | INTRODUCTION

International conservation targets aim to protect species and ecosystems in the face of climate change and human land use pressures. The Convention on Biological Diversity (CBD) forms the international basis for national level targets to reduce biodiversity loss, including the protection of ≥17% of terrestrial areas (Aichi Biodiversity Target 11; CBD, 2010). Networks of protected areas (Hannah, 2008) are essential in supporting biodiversity in the face of climate change. However, the protection of biodiversity often conflicts with socio-economic pressures in ecosystems such as forests, where human demographic changes increase the conversion of natural forest and demands for forest goods and services (Millennium Ecosystem Assessment, 2005). Protected area allocation is therefore constrained by socio-economic conditions. The extent of protection required to prevent biodiversity loss, particularly in the face of climate change which is expected to exacerbate the negative impacts of land use change (Mantyka-Pringle et al., 2015), needs to be assessed to inform habitat management and resource exploitation.

Forests are important globally because of their biodiversity, ecosystem services and economic resources (Gauthier, Bernier, Kuuluvainen, Shvidenko, & Schepaschenko, 2015). The intensive exploitation of forests leads to loss of old-growth forests and, subsequently, biodiversity loss (Gauthier et al., 2015). To reduce such negative impacts, legally protected and voluntarily set-aside forest can be designated with the aim of allowing forest to develop naturally. This results in the accumulation of dead wood (Hedwall & Mikusiński, 2015) which is a key resource for forest biodiversity (Müller & Bütler, 2010; Stokland, Siitonen, & Jonsson, 2012). Set-aside forest is likely to be an essential source of dead wood, as decomposition rates are predicted to increase in response to climate change, reducing the length of time dead wood is available (Mazziotta et al., 2014). Furthermore, it has been shown that for an old-forest indicator species, setting-aside forest from production could facilitate an increase in occurrences at the species southern range edge, despite climatic changes (Mair et al., 2017b). While reserves could buffer species against the effects of climate change, efficacy is likely to vary among species (Gaüzère, Jiguet, & Devictor, 2016). Thus, it is unknown whether a range of forest species with varying ecological requirements and red-list status would benefit differently from set-aside forest under climate change.

Despite the important interactive effects of land use and climate change in driving biodiversity change (Mantyka-Pringle et al., 2015), previous work projecting biodiversity responses has largely focused on forecasting climate change impacts, and land use changes have been neglected (Titeux et al., 2016). In many cases, this may be due to a lack of realistic projection scenarios comprising land use data directly relevant to species occurrences (Martin, Van Dyck, Dendoncker, & Titeux, 2013). There is therefore a lack of knowledge of how conservation strategies such as setting-aside forest from production could modify climate-induced biodiversity losses at large geographical scales. Moreover, it is unclear how the relative importance of land use and climate change effects on biodiversity may vary over time (Pawson et al., 2013). The lack of large-scale and long-term data for specialist species, such as old-growth forest saprotrophic fungi, was previously limiting, meaning that interspecific variation in responses to macroclimate and resource availability is little understood (but see Abrego, Christensen, Bässler, Ainsworth, & Heilmann-Clausen, 2017). The increasing availability of spatially and temporally extensive citizen science data now facilitates species distribution modelling to address such issues (Devictor, Whittaker, & Beltrame, 2010), but we are not aware of any large-scale, long-term forecasts of variation in interspecific response to realistic, combined land use and climate scenarios.

In this study, we forecast the responses of six old-forest indicator species to a range of forest management and climate change scenarios. The study species are functionally important dead wood-decaying fungi, which are negatively affected by forestry (Berglund, Hottola, Penttilä, & Siitonen, 2011) and are indicators of habitats of conservation value (Halme, Holec, & Heilmann-Clausen, 2017; Heilmann-Clausen et al., 2015). Dead wood-decaying fungi are an under-studied group, and there is currently limited understanding of their likely responses to future macroclimate and forest changes (but see Mazziotta et al., 2016). Here, we use an ensemble of species distribution models for each species based on citizen science to project species-specific habitat suitability in response to a range of forest management and climate scenarios. We test (1) the impact of different climate change scenarios, (2) the effect of increasing the area of forest set-aside from production and (3) whether forest management has the potential to facilitate an increase in habitat suitability at the southern range edge for all six study species, despite climatic changes.

2 | METHODS

2.1 | Study species

We studied six old-forest indicator species of wood-decaying fungi; *Amylocystis lapponica* (abbreviated to amylap), *Fomitopsis rosea* (fomros), *Phellinus chrysoloma* (phechr), *Phellinis ferrugineofuscus* (phefer), *Phellinus nigrolimitatus* (phenig) and *Phlebia centrifuga* (phlcen). Old-forest indicator species are sensitive to habitat change due to their specific habitat requirements, and so their presence provides information on the conservation value and ecosystem functioning of forest stands (Heilmann-Clausen et al., 2015). All six species are associated with Norway spruce and in Sweden occur primarily in the boreal region (Figure 1). *A. lapponica* and *P. centrifuga* are classified as vulnerable (VU) while the remaining species are near threatened (NT) in Sweden according to the criteria of the IUCN (Artdatabanken, 2015). The species vary in their fruit body morphology and lifespan, spore shape and volume, hyphal system, decay type, log-decay-diameter specificity, natural abundance and habitat-connectivity dependency, but are all associated with old-growth spruce forest and so are negatively affected by forestry (Berglund et al., 2011; Nordén, Penttilä, Siitonen, Tomppo, & Ovaskainen, 2013; Stokland et al., 2012).

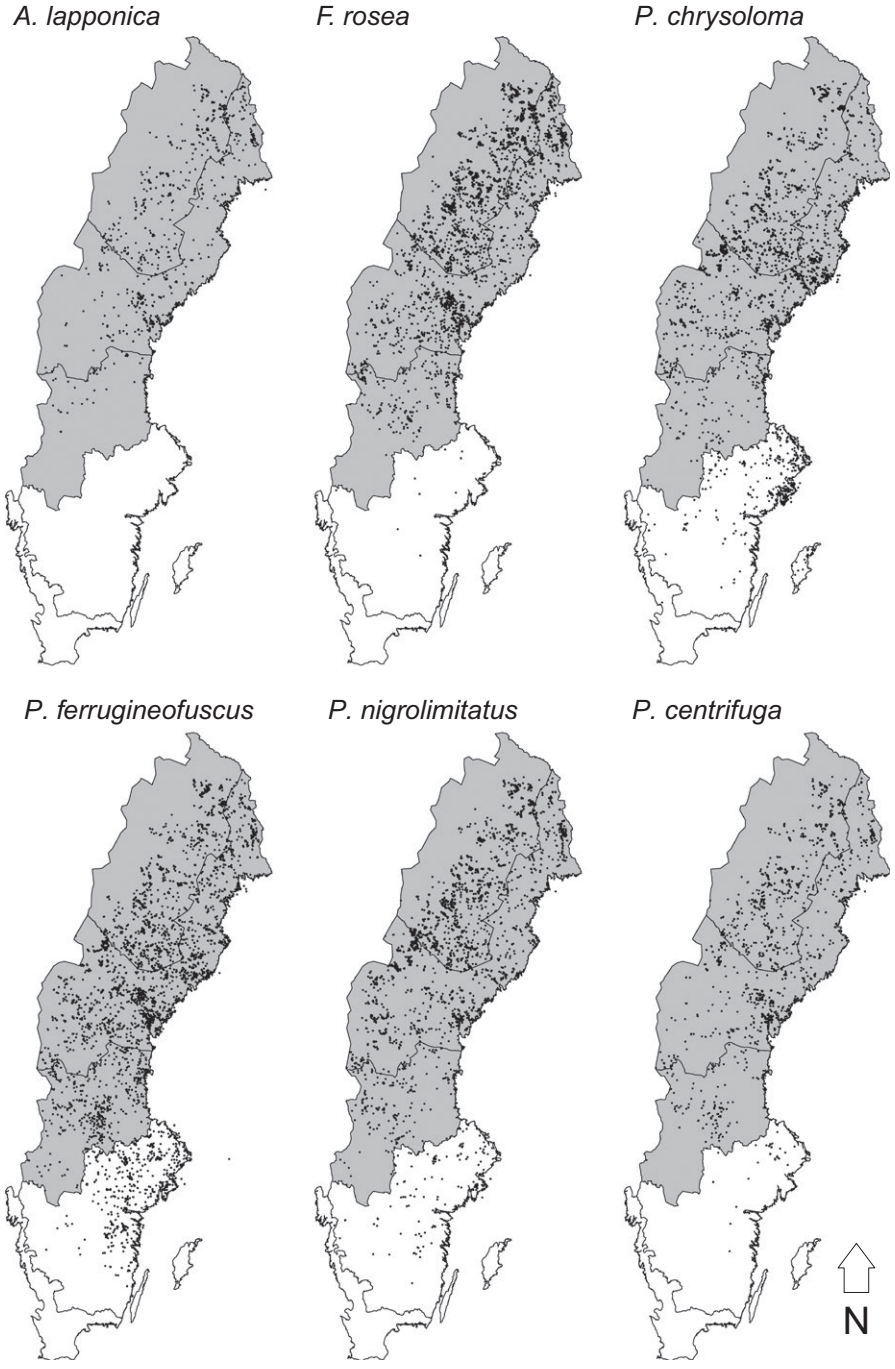

FIGURE 1 Observed 100 m grid cell resolution occurrences of the six study species in 2000–2013, obtained from Swedish Lifewatch (analysisportal.se). The northern boreal region is shown in grey and the southern boreo-nemoral region is white

2.2 | Species observation data

We used citizen science observation data from the Swedish open-access Lifewatch website (www.analysisportal.se) for the species distribution models. Data were for the period 2000–2013 at the 100 m grid cell resolution. The observation data were presence-only (PO; number of observations given in Table S1.1); however, we established presence–absence (PA) data based on observation records from eight methodical recorders (see Mair et al., 2017a for details). We also established repeat-visit detection/non-detection data based on presence-only records of 35 old-forest indicator species of dead wood-dependant fungi. For this, the detection of indicator species other than the focal species represented the non-detection of the focal species [see Mair et al., (2017a) for details].

We used observation data from Sweden only to fit models although the six study species are distributed across northern Europe (Ryvarden & Melo, 2014). This is due to data limitations and in Appendix S2, we justify our focus on the extent of species occurrence in Sweden for fitting the models.

2.3 | Species distribution models

For each species, we fitted five species distribution models (SDMs) to citizen science data (CSD) observations. The models applied were

as follows: a Generalized Linear Model (GLM) using PA data; a point-process Poisson model using both PA and PO data (here termed the PA/PO model; Fithian, Elith, Hastie, & Keith, 2015), a Bayesian occupancy model using repeat visit data (Kéry, Gardner, & Monnerat, 2010), MaxEnt using PO data with a random background (Phillips, Anderson, & Schapire, 2006) and MaxEnt using PO data and the target group background (TGB) approach (Phillips & Dudik, 2008).

Species occurrence was modelled as a function of living spruce volume, connectivity to old spruce forest (≥100 years), mean annual temperature (averaged over 1989–2010), summed precipitation May–November (averaged over 1989–2010) and a wetness index (Appendix S1). Based on a biological understanding of the species, we tested for linear effects of all variables, with the exception of the wetness index, for which we also tested a quadratic term. We also tested temperature–precipitation, spruce volume–temperature and spruce volume–precipitation interactions. Model selection procedures followed the same methods as applied in Mair et al. (2017a); details are given in Appendix S1. Mair et al. demonstrated that, for *P. ferrugineofuscus*, an ensemble of models based on CSD was able to reproduce species projections from a Bayesian state-space model for colonization–extinction dynamics based on systematically collected field data. Here, we apply the same SDM ensemble approach and extend these methods to a group of ecological similar and equally easily identifiable species.

2.4 | Forest management scenarios

We used the SDMs to project species habitat suitability in response to forest management and climate change scenarios. In these scenarios, areas of forest set-aside from production are classified as (1) legally protected reserves, (2) forest voluntarily set-aside from production for biodiversity conservation (Simonsson, Östlund, & Gustafsson, 2016) or (3) retention forest, where part of the forest stand is left unlogged while the rest is cleared (Gustafsson et al., 2012). The 'baseline' scenario assumes that over the coming 100 years, 3.6% of forest is set-aside from production as legally protected reserves, reflecting the current extent of legal protection. The remaining forest is used for timber production and 100% of tree growth is cut. Tree growth rates were assumed to depend upon climate (and overall were projected to increase with increasing climate change; Eriksson et al., 2015). We applied three climate scenarios to this baseline forest management scenario. These were (1) constant present day climate (*3.6% Const*), (2) representative concentration pathway (RCP) 4.5 (*3.6% RCP4.5*) and (3) RCP 8.5 (*3.6% RCP8.5*; see Section 2.5 below for details) (Table 1).

To test whether increasing the amount of land set aside from forestry made a significant improvement to future species habitat suitabilities, we applied a scenario which increased the total amount of forest set-aside from production to 16% through the addition of voluntarily set-aside and retention forest. Land use was thus changed from forestry management to conservation, which means simulating almost exclusively natural local-scale forest dynamics. Sixteen percent set-aside is based on scenarios projected in the Swedish Nationwide Forestry Scenario Analysis 2015 (Eriksson, Snäll, & Harrison, 2015) and is close to the Aichi Biodiversity Target 11 aim of protecting ≥17% land. For this scenario, we assumed RCP 4.5 (*16% RCP4.5*; Table 1). To test an even larger increase in conservation effort, we increased the total amount of forest set-aside to 32% (*32% RCP4.5*). This 32% comprised 7.2% legally protected reserves, and the remainder voluntarily set-aside and retention forest. This gave a total of five forest and climate change scenarios (Table 1).

TABLE 1 Layout of the experimental design based on two factors: amount of forest set-aside from production and climate, and the corresponding scenario acronyms

	Climate		
Set-aside forest area	Constant present day climate	RCP4.5	RCP8.5
3.6%	*3.6% Const*	*3.6% RCP4.5*	*3.6% RCP8.5*
16%	–	*16% RCP4.5*	–
32%	–	*32% RCP4.5*	–

The initial numbers of the acronym indicate the percentage of forest area set-aside from production, and then the climate scenario is given (*Const* is constant present day climate).

Forest projection data were available from the Swedish Nationwide Forestry Scenario Analysis 2015 (Claesson, Duvemo, Lundström, & Wikberg, 2015; Eriksson, Snäll, et al., 2015). Projections were available for a total of 29,892 National Forestry Inventory (NFI) plots (Fridman et al., 2014) located across Sweden. Projection data were available for each plot for every fifth year from 2020 to 2110 (for details see Appendix S3).

2.5 | Climate change scenarios

The climate change scenarios applied were RCP 4.5, which assumes a radiative forcing of 4.5 Wm^{-2} by 2100 and is representative of an intermediate future energy-use scenario, and RCP 8.5, which assumes a radiative forcing of 8.5 Wm^{-2} by 2100 and is representative of a highly energy-intensive scenario (van Vuuren et al., 2011). For both RCP scenarios, five different global climate models were used from the CMIP5 archive (Taylor, Stouffer, & Meehl, 2012; see Appendix S3 for details). We used monthly total precipitation summed over the period May–November, and monthly mean temperature data averaged across each year, to match the climate variables used during SDM fitting. We matched the forest scenario assumptions to the climate change scenarios (Table 1). For the scenario with constant present day climate (*3.6% Const*), we applied the observed climate data for the present day (1980–2010 averages) which were the data used for model fitting.

2.6 | Species projections in response to forest and climate scenarios

For each species, we used each of the five SDMs to project species habitat suitabilities in response to the scenarios of forest

management and climate change (Table 1). MaxEnt models predict relative suitability, while the other models predict probability of occurrence; therefore, we use the general term 'habitat suitability' throughout. For scenarios incorporating climate change, projections were made for each of the five climate projection models separately.

We applied mechanistic assumptions to incorporate aspects of the species' ecology which were not captured in the correlative structure of the models (Kearney & Porter, 2009). Firstly, the species could not occur in plots where there was no dead wood (Mair et al., 2017a). Secondly, species could not occur in plots where the forest age was between a species-specific range (see Appendix S4 for thresholds). Thirdly, occurrence probabilities in retention forest were reduced to one-tenth of the projected values, to account for edge effects in forest fragments. The reduction level was based on a clear past (Ruete, Snäll, & Jönsson, 2016) and future (Ruete, Snäll, Jonsson, & Jönsson, 2017) gradient of this group of species from clear-cut edge into woodland key habitats with a median of six hectares. Retention patches are, however, generally much smaller than six hectares (Lämås, Sandström, Jonzén, Olsson, & Gustafsson, 2015) and so a uniform reduction of one-tenth across retention plots was applied to capture edge effects.

Following the application of mechanistic assumptions, for scenarios incorporating climate change, projected habitat suitabilities for each species from the SDMs were averaged across the five climate projection models. Projections of habitat suitability at each plot were then scaled up to reflect the area of land that each NFI plot represents, accounting for the uneven distribution of plots across the country. Finally, we took an ensemble modelling approach by averaging across projections from the five species distribution models. Results are presented as mean habitat suitabilities and as relative change over time from 2020.

We tested whether increasing the amount of forest set-aside from production from 3.6% to 16% through the addition of voluntary set-asides and retention forests had a significant effect on projections. To do this, we tested the difference between the projected mean habitat suitabilities in 2100 using a Generalized Linear Model (GLM) specified with a quasibinomial distribution and including study species and SDM type as factors. We present differences as the percentage change in mean suitabilities when the amount of forest set-aside was increased from 3.6% to 16%. We then repeated this analysis to test the effect of increasing the amount of forest set-aside from 3.6% to 32%.

We tested the potential for forest management to facilitate an increase in species habitat suitabilities in the southern boreo-nemoral region. We tested the difference in overall mean habitat suitabilities between the boreal and boreal-nemoral regions, for 2020 and 2100 separately, using a GLM specified with a quasibinomial distribution and including study species, scenario and SDM type as factors. We then tested whether, by the end of the projection period, mean habitat suitabilities were projected to increase in the boreo-nemoral region to such an extent that the region was as suitable for the study species as the boreal region. To do this, we used species-specific GLMs to test the difference in mean habitat suitabilities between the boreal region in 2020 and the boreo-nemoral region in 2100, specifying the GLMs with a quasibinomial distribution and including scenario and SDM method as factors.

2.7 | Assessing the predictive ability of species distribution models

We tested the predictive ability of the frequentist SDMs by applying fivefold block cross-validation and calculating the area under the receiver operating curve (AUC; see Appendix S1 for details). For the Bayesian occupancy models, data limitations meant that we instead tested the predictive ability by predicting species occurrence across the PA data set (see Appendix S1).

3 | RESULTS

3.1 | Best-fitting species distribution models

The best-fitting SDMs for all species included a significant positive effect of living spruce volume and a significant negative effect of temperature on species occurrence (Table S6.4 in Appendix S6). The inclusion and effects of other variables varied among models and species (Table S6.4). Precipitation had a negative effect for all species except for *A. lapponica* for which the effect was positive and *P. nigrolimitatus*, for which the effect varied. Connectivity was often significant and had a positive effect on species occurrence. Significant interactions between forest and climate variables were found, but these varied among models and species (see Table S6.5 in Appendix S6 for an analysis of variance addressing sources of uncertainty in the projections).

3.2 | Projected species responses to climate change and varying extents of set-aside forest

With 3.6% of forest allocated as legally protected reserves and constant present day climate (*3.6% Const*), habitat suitabilities were projected to increase for all study species; the projected relative increase among species from 2020 to 2100 was 23% to 56% (mean 45%) across the study region (Figure 2a). These overall increases were driven by positive trends in legally protected reserves (Figure 2b), where increases in living spruce volume, dead wood volume and forest age were projected (Figure S5.7a in Appendix S5). In contrast, the majority of species were projected to show little change or to decline in production forest (Figure 2c).

With the inclusion of climate change, all six species were projected to show overall declines under RCP 4.5 (*3.6% RCP4.5*: mean −42%, range −59% to −6%) and greater declines under RCP 8.5 (*3.6% RCP8.5*: mean −70%, range −85% to −37%) (Figure 2a). These declines were due principally to the projected increase in temperature (temperature increase is greater under RCP8.5 than RCP4.5; Figure S5.8), as the occurrence of all study species showed a negative relationship with temperature (Table S6.4).

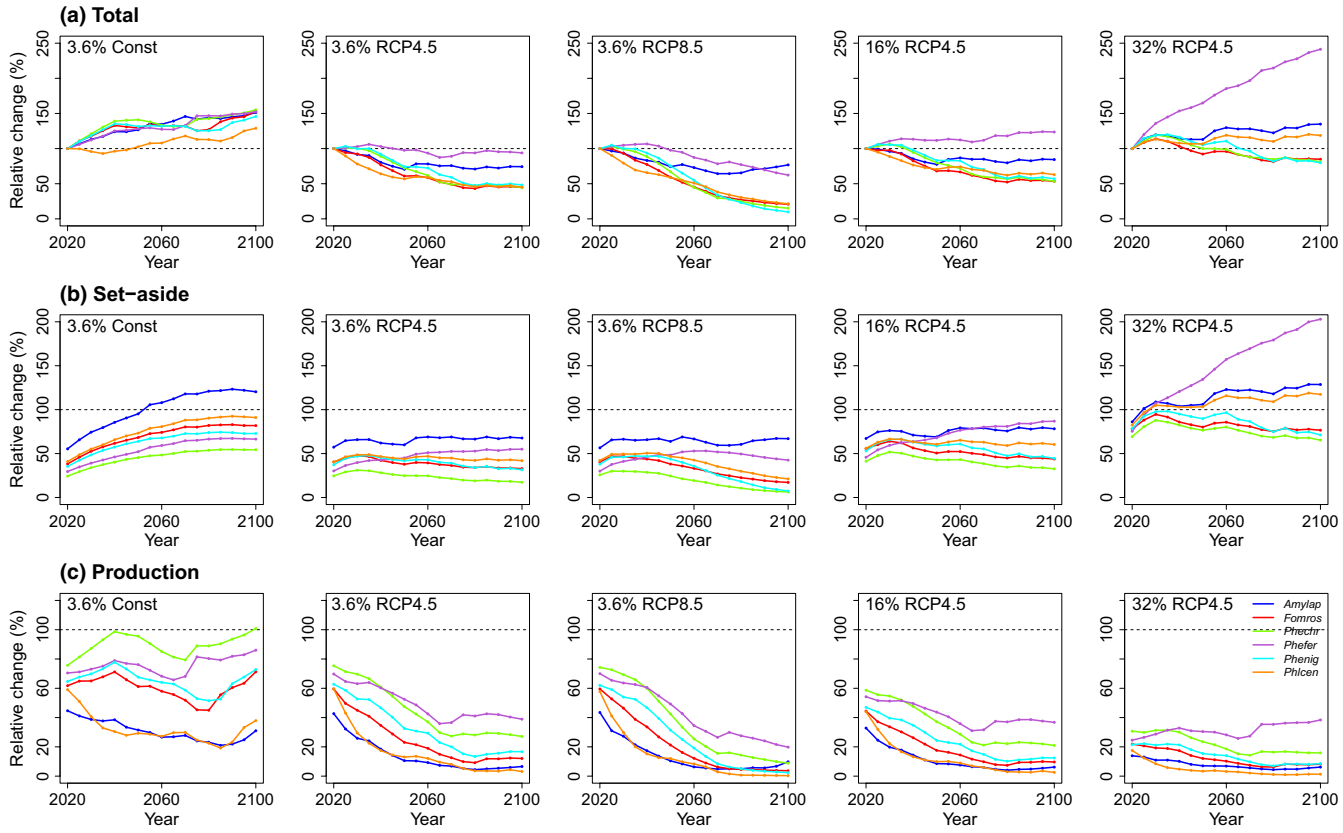

FIGURE 2 Relative change in projected habitat suitabilities for the six study species in response to five forest management and climate change scenarios. Results are separated into relative change across the whole study area for (a) all forest, (b) forest set-aside from production, and (c) production forest. The dashed black line shows the total habitat suitability in 2020, against which relative change is calculated. Species abbreviations are given in Section 2.1, and scenario abbreviations in Table 1. Note the varying *y*-axes among (a–c)

Habitat suitabilities in production forest were projected to decline under climate change. Habitat suitabilities in set-aside forest were projected to increase over the first one to two decades and then remain relatively constant under RCP 4.5, or decline slightly under RCP 8.5 (Figure 2b). Set-asides therefore reduced the overall rate of decline for most species under climate change. Forest changes were the predominant driver of changes in habitat suitabilities at the start of the projections, before the negative impacts of climate change took effect and limited habitat suitabilities further into the future.

Increasing the amount of set-aside forest to 16% through the addition of voluntarily set-aside and retention forest resulted in more positive projected trends under climate change (RCP 4.5); one species, *P. ferrugineofuscus*, showed an overall increase (*16% RCP4.5*: mean −28%, range −51% to 20%; Figure 2a). Increasing the total amount of set-aside forest to 32% resulted in three species showing an overall increase (*32% RCP4.5*: mean 25%, range −21% to 126%; Figure 2a). For both scenarios, the more positive trends in set-aside forest were the driving force behind the more positive trends overall (Figure 2). Species were again projected to show an increase in set-aside forest over the first one to two decades, driven by forest changes, before the negative impacts of climate change predominated. The exception was *P. ferrugineofuscus*, which showed a continuous increase in habitat suitabilities in set-asides under *32% RCP4.5*, suggesting that forest changes consistently had a stronger effect than climatic changes for this species under this scenario (Figure 2b).

Increasing the amount of forest set-aside from production resulted in a significant increase in overall projected species habitat suitabilities by 2100 (GLM effect of increasing set-aside forest from 3.6% to 16%, $T = 7.56$, $p < .001$; GLM effect of increasing set-aside forest from 3.6% to 32%, $T = 14.50$, $p < .001$). However, there were differences among species in the relative benefit (Figure 3). Within each scenario, *P. centrifuga* was projected to show the largest relative benefit from an increase in set-aside forest, followed by *P. ferrugineofuscus* and then *A. lapponica* (Figure 3).

Examination of the mean projected habitat suitabilities in 2020 and 2100 for legally protected reserves, voluntary set-aside, retention and production forest separately, showed that production forest had very low suitabilities for all six study species (Figure S7.9 in Appendix S7). Legally protected reserves had the highest suitabilities for each species, followed by voluntary set-aside forest (Figure S7.9).

3.3 | Differences in projected species responses between the boreal and boreal-nemoral regions

For all species and scenarios, overall mean habitat suitabilities were substantially higher in the boreal region compared to the boreo-nemoral region in 2020 (GLM effect of region, $T = -31.84$, $p < .001$;

Figure 4). In 2100, mean suitabilities remained higher in the boreal compared to the boreo-nemoral region for all species and scenarios (GLM effect of region, $T = -16.28$, $p < .001$). However, temporal changes within regions varied among species (Figure 4).

Phellinis ferrugineofuscus was the only species for which projected habitat suitabilities in the boreo-nemoral region in 2100 were not significantly different to the habitat suitabilities in the boreal region in 2020 (species-specific GLM, boreal-nemoral in 2100 against boreal in 2020, $T = -1.14$, $p = .26$). In other words, by 2100, habitat suitabilities in the boreo-nemoral region were similar to habitat suitabilites in the boreal region in 2020 for this species across all scenarios. For the remaining species, habitat suitabilities were significantly lower in the boreal-nemoral region in 2100 compared to the boreal region in 2020 (species-specific GLMs, boreal-nemoral in 2100 against boreal in 2020, for all species $p < .001$). This was due to interspecific differences in the fitted SDMs; *P. ferrugineofuscus* was the only species for which living spruce volume had the largest estimated coefficient across all SDM types, indicating that spruce volume had a stronger effect than climate on habitat suitability (Table S6.4). However, the large error bars in Figure 4 indicate variation among SDMs in the relative importance of climate and forest variables in determining species occurrence (Tables S6.4 & S6.5).

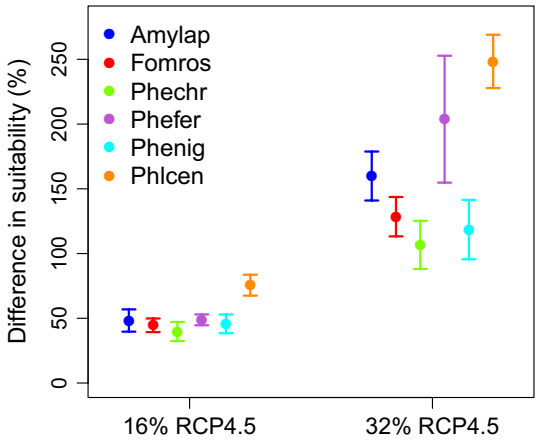

FIGURE 3 The relative benefit to the study species of increasing the amount of forest set-aside from production from 3.6% to 16% and 32% through the addition of voluntary set-aside and retention forest. For each species, the difference shown is the percentage increase in mean habitat suitabilities projected in 2100 when the amount of forest set-aside is increased from 3.6%. Species abbreviations are given in Section 2.1, and scenario abbreviations in Table 1

3.4 | Assessing predictive ability of species distribution models using withheld observation data

Mean training AUCs for the four frequentist SDMs varied between 0.77 and 0.84 and mean testing AUCs varied between 0.76 and 0.82 among species (Table S8.6 in Appendix S8). For occupancy models, training AUCs calculated on data used in model fitting were 0.64–0.73 and testing AUCs calculated on the presence–absence data were 0.69–0.84 (Table S8.6).

4 | DISCUSSION

Our projections show that changing land use could reduce future climate change threats for some old-growth forest indicator species.

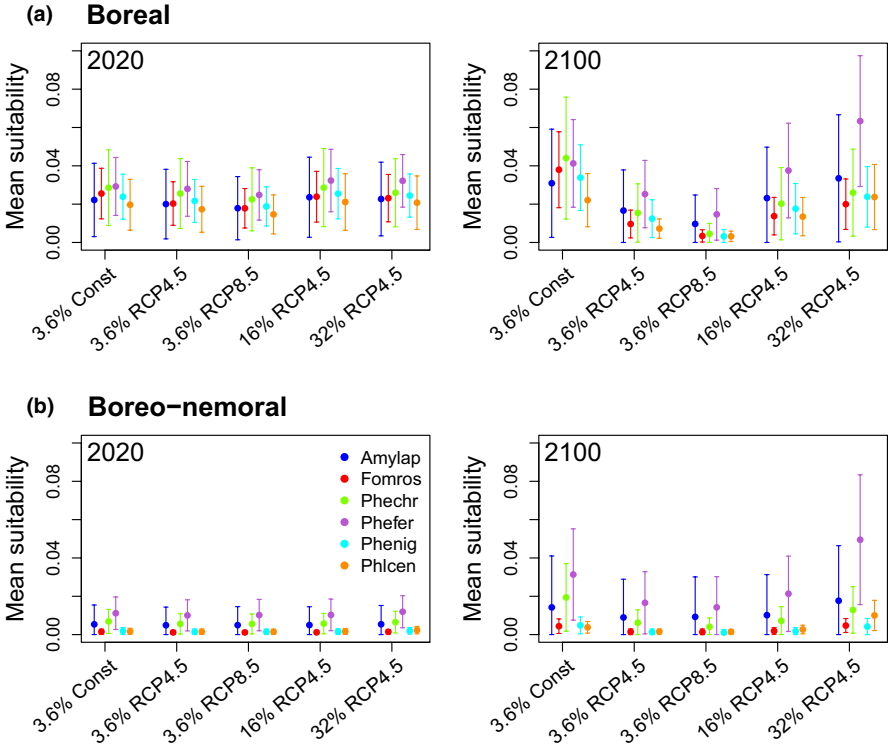

FIGURE 4 The mean ± *SD* projected habitat suitabilities for each species overall in (a) the boreal region and (b) the boreo-nemoral region, in the first year of the projections (2020) and the last year (2100). Species abbreviations are given in Section 2.1, and scenario abbreviations in Table 1

For six species of fungi in an intensively managed landscape, we found that designating 3.6% of forest as legally protected reserves over the coming century was likely to be insufficient to maintain habitat suitabilities, and therefore population sizes, under climate change. Assuming RCP 4.5 (intermediate–low emissions), habitat suitabilities for all six species were projected to decline over time, with even greater declines projected under RCP 8.5 (high emissions). Increasing the amount of forest set-aside from production to 16%, which is close to the Aichi Biodiversity Target 11 aim of ≥17% of land protected (CBD, 2010), resulted in a projected increase for one species under intermediate emissions (RCP 4.5), while an increase to 32% forest set-aside resulted in projected increases for three of the six species. Hence, changing land use by increasing the amount of old-forest set-aside could reduce future threats from a warming climate for these highly specialized and rare fungi. Setting aside as much as one-third of productive forest is likely to be politically unrealistic in intensively managed landscapes; however, conditions are still improved and a smaller subset of species may still avoid declines at the lower level of 16% set-aside, which is more achievable in practice.

The negative impact of climate change is due to the sensitivity of the study species to macroclimate, and specifically to the negative relationship between species occurrence and temperature. This is the first large-scale study, using models that operate at small spatial scale (100 m), to quantify and project such a strong future negative effect from climate warming for fungal species. Our study investigates macroclimatic effects; due to the spatial and temporal resolution of the climate data used, interannual climatic variability and microclimatic effects could not be captured. There is some evidence to suggest that microclimatic effects may override the effects of resource availability on species occurrence at a local scale (Bässler, Müller, Dziock, & Brandl, 2010). However, effects of climate change on fungal species composition have been detected (Andrew et al., 2016) and mechanistically, macroclimate is likely to effect the habitat suitability of wood-rotting fungi due to increased rates of dead wood decomposition causing a reduction in resource availability (Mazziotta et al., 2014, 2016). Variation among studies may be partly because wood-inhabiting fungi exhibit interspecific variation in responses to macroclimate and resource availability (Abrego et al., 2017) and our results, based on large-scale citizen science data, show that this produces interspecific variation in projected trends.

Our results also suggest that the relative importance of climate and forest in determining habitat suitability for the study species is likely to show temporal variation. Under constant present day climate with 3.6% set-aside, all six study species showed an almost continuous increase in habitat suitability in set-aside forest, in response to an increase in spruce volumes and forest age. However, when assuming RCP 4.5 or RCP 8.5, projected habitat suitabilities either remained constant or began to decline after an initial increase, indicating that climate change became the predominant driver of habitat suitability. An increase in the amount of forest set-aside from production to 32% resulted in *P. ferrugineofuscus*, *P. centrifuga* and *A. lapponica* showing relatively continuous increases in set-aside forest. *P. ferrugineofuscus* is the least specialized of the six study species in terms of its dead wood niche and it is also the species which occurs most frequently on its preferred dead wood type (Nordén et al., 2013). Further analyses would be required to determine the extent to which species traits can explain differences among species responses to changes in the availability and connectivity of set-aside forest. Some species may benefit from a combination of species-specific dispersal, colonization and establishment traits, and for example, species traits such as spore type may influence wind dispersal (Nordén et al., 2013).

Interspecific variation in sensitivity to climate and forest conditions also resulted in interspecific variation in projected distributional changes under climate change. *P. ferrugineofuscus* was the only species to show the potential to increase in abundance in the southern boreo-nemoral region in response to maturing forest in set-asides. For *P. Ferrugineofuscus*, spruce volume was the most important determinant of species occurrence; for the remaining five study species temperature was the most important and therefore these species were limited by climate. Our results suggest that *P. ferrugineofuscus* may be the only study species whose current rarity in the boreo-nemoral region is primarily driven by the history of intensive forestry (Mair et al., 2017b). This species therefore has the potential to increase in occurrence at its southern distribution edge in Sweden, given appropriate forest management, in contrast to the other study species which may follow the expected trend of a northwards retreat under climate change.

Projected trends provide clear evidence for the positive impact of increasing the amount of forest set-aside from production on overall habitat suitabilities for all six of these old-forest indicator species. When the amount of forest set-aside from production was increased from 3.6% to 16%, we found a significant increase in habitat suitabilities for each species by 2100. However, five of six species were still projected to show overall declines, albeit smaller declines than projected with only 3.6% forest set-aside. This suggests that, under climate change, the Aichi Biodiversity Target 11 of ≥17% of habitat protected may be insufficient for species sensitive to the intensive exploitation of their habitat. When the amount of forest set-aside was increased to 32%, overall increases in habitat suitability were projected for half the study species, with the remaining species showing slight declines. Previous research has suggested that species richness declines below the threshold of around 30% of natural habitat remaining in a landscape (Andrén, 1994). Our results suggest that a natural habitat threshold of ≥30% may be sufficient to prevent declines under climate change for some, but not all, dead wood decaying fungal species. A high investment in climate change aware conservation is therefore likely to be necessary in exploited landscapes. Moreover, given the initial positive responses of species to maturing forest in set-aside, before the negative effects of climate change took effect, an early investment in conservation is likely necessary to increase species resilience to climate change in the long term.

We make the recommendation to land managers that, at the national scale, the amount of forest set-aside from production be increased beyond the Aichi Biodiversity Target 11 aim of ≥17%. Early investment in conservation is likely to reduce the negative impacts of climate change on habitat suitabilities in the future; while there are many uncertainties surrounding climate change effects, there is clear evidence for the positive effects of conservation action. We conclude that old-forest fungal indicator species are likely to suffer declining habitat suitabilities under climate change, but that these negatives effects can be at least reduced through setting-aside forest from production. The benefits, however, of conservation efforts are likely to vary among species due to interspecific variation in climate sensitivities and habitat associations.

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DATA ACCESSIBILITY

Data associated with this paper have been deposited in the Environmental Climate Data Sweden depository https:/doi.org/10.5879/ECDS/2017-03-23.1/1.

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BIOSKETCH

The authors have diverse specializations and interests, and collaborate to address land use and climate change impacts on biodiversity in forest landscapes.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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